

BODY SIZE IN NORTH AMERICAN LEPIDOPTERA AS RELATED TO GEOGRAPHY

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ABSTRACT. Body-size patterns among eight main regions and subregions of North America are established with species-level entities in 37 genera and 18 families of Lepidoptera. Patterns are compared with expectations arising from certain underlying causes of body size variability. Main regions are East, West, North, South; subregions are Northeast, Northwest, Southeast, and Southwest; all are defined by latitude 40°N and longitude 100°W. Published wing measure, either forewing or span length, serves as an index of body size. Heat-transfer principles determining thoracic temperatures necessary for flight suggest that diurnal genera should converge on medium body size at high latitudes and high elevations. The large-bodied *Papilio* (Papilionidae) actually do so in the North and West, and perhaps *Hesperia* (Hesperiidae) also, the West having higher elevations than the East. Three other diurnal genera of medium body size vary little in size geographically as might also be expected from heat-transfer principles. Among 32 nocturnal genera surveyed, no distinct latitudinal pattern in body size is evident, nor does prior knowledge predict one. Prior positive relations between altitude of capture site and body size in Tortricidae suggest that nocturnal moths generally might prove larger-bodied in the West because of higher elevations. Nearly all the nocturnal genera do show distinct longitudinal body-size variation, 30 of 32 genera being larger in the West by a mean 16% in wing measure. This longitudinal regularity suggests a new ecogeographic size rule. No unequivocal explanation for the underlying altitudinal increase in body size of nocturnal lepidopterans has yet emerged, but higher food-plant quality at higher elevations is a likely factor.

Additional key words: biogeography, wing measure, latitude, longitude, altitude.

The idea that body size in North American Lepidoptera is related to geography arose more than a century ago. Packard (1876) claimed that Colorado and Pacific Coast specimens of some two dozen species of Geometridae were larger bodied than Atlantic Coast specimens. Later he reported similar variation in several species of Notodontidae (Packard 1895).

Longitude was the geographic dimension involved in these early observations. Since Packard's time, knowledge of insect body size as related to longitude has progressed but little. Modern observations of longitudinal effects on lepidopteran body size are scant and refer to a mere handful of species. A few authors have noted statistical correlations between longitude and body measurements such as forewing length, or have incidentally noted longitudinal changes in forewing length, or included data that show such changes. The magnitude of longitudinal change in wing length in these reports ranges from 10 to 18%; the species involved are *Pontia protodice* (Boisduval & Leconte) (Pieridae) (Abbott et al. 1960), *Dichomeris gleba* Hodges (Gelechiidae) (Hodges 1986), *Autochton cellus* (Boisduval & Leconte) (Hesperiidae) (Burns 1984), *Euxoa c. churchillensis* (McDunnough) (Noctuidae) (Lafontaine

1987), and *Hyalophora columbia* (Smith) (Saturniidae) (Collins 1973), data for the last-named also having a latitudinal component. In all these observations, as in Packard's, body size is larger in the West than in the East.

In Lepidoptera, measures such as forewing length and span can be taken as reliable indexes of body size up to family level (Miller 1977b, Wasserman & Mitter 1978, and others). Throughout this paper, I use wing measure and body size as interchangeable concepts.

As for latitudinal effects, Packard reported none, although he was aware of the latitudinal size gradients in homeotherms now known as Bergmann's and Allen's rules. These ecogeographical rules state, respectively, that overall body size increases from south to north whereas body extremities like ears and tails diminish (Allee & Schmidt 1951). The concept of latitude as a possible factor in insect body size arose later than longitude and apart from it. Field and laboratory observations show some nonlepidopterous insects superficially conforming to Bergmann's rule, and some not (Ray 1960). In Lepidoptera, sweeping statements have been made about latitudinal body-size effects: "The generally recognized north-south trend for increase in size in Great Lakes butterflies seems to be associated mainly with non-migratory species. Members of such butterfly genera as *Papilio*, *Pieris*, *Cercyonis*, *Euptychia*, *Lethe*, *Boloria*, *Speyeria*, *Erynnis*, *Hesperia*, and *Poanes*, for example, tend to show southward size increases. Similar observations may be made in certain moths, such as the saturniids *Eacles*, *Antheraea*, and *Hyalophora*" (Wagner & Hansen 1980). Some of these trends may be expected for lepidopterans, as discussed below, but few have been actually demonstrated.

Bergmann's and Allen's rules for homeotherms are now explained as heat-conserving surface/mass adjustments to latitudinal temperature gradients (Mayr 1976, Vernberg 1962). Similarly, studies of butterfly body heat capacity and thoracic temperatures necessary for flight lead to the conclusion that butterflies should converge on an optimum size at arctic latitudes (Douglas 1986). This convergence may proceed in opposite directions depending on characteristic body size: from large to medium as in *Parnassius phoebus* (Fabricius) (Papilionidae) (Guppy 1986) and *Papilio glaucus* Linnaeus (Papilionidae) (Scriber 1982); or from small to medium, as in *Pieris napi* (Linnaeus) (Pieridae) (Wagner & Hansen 1980). If body size is already optimal for northern latitudes, it may not change at all latitudinally, as in *Pontia protodice* (Abbott et al. 1960). Critical limits cannot be stated for the three butterfly body-size classes because factors other than size are also involved.

Butterflies also show a body-size response to altitude. The explanation seems much the same as that for the latitudinal response described

above, namely body heat capacity (Douglas 1986). As expected for characteristically large-bodied butterflies, negative correlations between altitude and body size are reported for *Occidryas chalcone* (Doubleday) (Nymphalidae) (Hovanitz 1942), *Parnassius phoebus* (Fabricius) (Guppy 1986), and *Polites draco* (Edwards) (Hesperiidae) (Brown 1962), the last without display of supporting data. On the other hand, in Tortricidae, which are nocturnal or crepuscular, a positive correlation exists between altitude of capture site and body size, an empirical finding thus far without unequivocal explanation (Miller 1991).

There has never been an attempt to put body size and geography into perspective for any large insect group like an order. I present here an order-wide survey of body size in North American Lepidoptera, and compare results with expectations derived from prior knowledge of body size variability. The survey examines body size indexes among four main regions and four subregions defined by longitude and latitude. My approach differs from those of the past for insects because species in multiregional genera provide most of the size data rather than populations in multiregional species. If populations within species exhibit geographic differences in body size, the factors responsible for such differences should produce them at the next two higher taxonomic levels in exactly the same way. Thus similar geographic differences in body size can be expected among subspecies in polytypic species, and among species in genera. This approach has been productive with vertebrates (Allee & Schmidt 1951, Ray 1960). Because properly defined genera are monophyletic, the species of a genus constitute an analogue of the populations within a species. Use of this analogue here yields ready-made body-size data because forewing length or span has been published for most species of North American Lepidoptera.

The literature reviewed above suggests that certain patterns should emerge from a geographic body-size survey of North American Lepidoptera. With respect to latitude, diurnal forms should increase, decrease, or remain the same in body size depending on their characteristic size. For nocturnal forms, there is no prior knowledge on which to base a latitudinal expectation. With respect to longitude, body-size patterns should reflect the differing elevations between East and West. Thus diurnal forms should show body-size patterns similar to those expected latitudinally, and nocturnal forms should show the increased body size associated with higher elevations in the West.

METHODS

This study surveys transcontinental, species-rich genera in which forewing lengths or spans are available for constituent species-group entities (species, subspecies, populations). Summary forewing lengths or spans are computed and compared within genera by the following

eight main regions and subregions of North America excluding Mexico: East, West, North, South, Northeast, Northwest, Southeast, Southwest. These regions and subregions are defined by latitude 40°N and longitude 100°W, map-lines which divide temperate North America into subequal halves and quadrants.

Genera were included in the survey if five or more constituent entities fell in each of the West and East main regions. The search for suitable genera was exhaustive, and no genus meeting the foregoing criterion was excluded. If more than one source of data for a genus was available, the most recent one was used, except that original reports were chosen in preference to later reviews or books based on them, and earlier treatments were chosen if later ones contained less precise wing measurements. Treatments published before 1940 were compared with the most recent Lepidoptera check list (Hodges et al. 1983) for current reliability; all included in the study had 95% or more of their entities still recognized taxonomically.

Entities were assigned to main regions and subregions in which their known ranges fell entirely or predominantly. Entities not falling predominantly in one subregion were not assigned to one, but were assigned to a main region if possible; entities not falling predominantly in either a subregion or main region were excluded from the study.

Northwest, Northeast, Southwest, and Southeast subregions are nested within North, South, East, and West main regions. Thus wing measurements for entities occurring in, say, the Northwest were included not only in the body-size computation for that subregion, but also in body-size computations for the North and West main regions.

Means of forewing length or span were computed for each genus in every main region and subregion encompassing five or more entities. The data entering these computations were entity means when available, but most commonly were midpoints of reported ranges, which approximate entity means. Separate ranges published for males and females were combined into a single entity range for midpoint determination.

Mean elevations were computed as described below from the *National Atlas* relief map, sheet No. 56, published by the Geological Survey, U.S. Dept. of Interior. Each main-regional and subregional mean is based on 50 or more altitudes obtained with transparent dot-grid overlays. Dots on overlays were evenly spaced, and spacing was chosen so that each subregion encompassed at least 50 dots.

Classification and nomenclature follow Hodges et al. (1983).

RESULTS AND DISCUSSION

Body-size means were computed in two or more main regions for 37 genera (Table 1). These data enable 37 East-West comparisons, 18

TABLE 1. Summary forewing lengths (L) or spans (S) (mm) by eight main regions and subregions of North America for 37 genera of Lepidoptera. Each value is a mean for five or more species-group entities computed chiefly from midpoints of published ranges. Boldface denotes a mean significantly larger than its East-West counterpart; italics, a mean significantly larger than its North-South counterpart (Student *t*-test, $P < 0.05$). Dashes denote fewer than five entities in a geographic partition or its counterparts.

Genus	Source	Measure	Geographic partition							
			W	E	N	S	NW	SW	NE	SE
Nepticulidae										
<i>Stigmella</i>	Wilkinson & Scoble 1979	L	5.6	4.3	—	—	—	—	—	—
Tischeriidae										
<i>Tischeria</i>	Braun 1972	S	7.8	7.0	—	—	—	7.8	—	6.8
Tineidae										
<i>Acrolophus</i>	Hasbrouck 1964	S	22.7	21.2	—	—	—	22.9	—	19.0
Lyonetiidae										
<i>Bucculatrix</i>	Braun 1963	S	7.9	8.0	7.7	7.9	8.2	7.8	7.4	8.2
Gracillariidae										
<i>Phyllonorycter</i>	Braun 1908	S	8.2	7.1	7.4	7.4	7.8	8.4	7.0	7.1
Oecophoridae										
<i>Agonopterix</i>	Hodges 1974	L	9.1	8.5	9.1	8.2	—	—	—	—
<i>Ethmia</i>	Powell 1973	L	9.4	9.4	—	—	—	9.0	—	9.2
<i>Antaeotricha</i>	Duckworth 1964	S	23.9	19.0	—	—	—	—	—	—
Elachistidae										
<i>Elachista</i>	Braun 1948	S	10.4	8.8	9.9	9.0	10.4	—	9.5	7.8
Coleophoridae										
<i>Batrachedra</i>	Hodges 1966	S	14.4	9.0	—	—	—	—	—	—
Gelechiidae										
<i>Dichomeris</i>	Hodges 1986	L	7.0	6.5	6.8	6.4	—	6.9	6.2	5.9
Argyresthiidae										
<i>Argyresthia</i>	Busck 1907	S	11.1	9.2	10.6	9.9	—	10.6	—	9.4
Sesiidae										
<i>Synanthedon</i>	Eichlin & Duckworth 1988	L	9.6	9.1	9.3	9.3	—	—	—	—
<i>Carmenta</i>	Eichlin & Duckworth 1988	L	7.9	8.3	—	—	—	7.8	—	8.1
Tortricidae										
<i>Olethreutes</i>	Heinrich 1926	S	17.4	14.5	—	—	—	—	—	—
<i>Rhyacionia</i>	Powell & Miller 1978	L	8.0	6.3	—	—	—	—	—	—
<i>Phaneta</i>	Heinrich 1923	S	17.0	15.5	17.5	16.8	17.6	16.8	16.6	—
<i>Eucosma</i>	Heinrich 1923	S	22.0	18.5	22.2	21.4	22.9	22.8	17.3	19.5
<i>Epiblema</i>	Brown 1973	S	16.9	15.8	17.0	15.4	—	—	17.5	14.9
<i>Epinotia</i>	Brown 1980	L	8.0	7.2	—	—	8.0	—	7.2	—
<i>Grapholita</i>	Heinrich 1926	S	12.6	10.7	—	—	—	—	—	—
<i>Cydia</i>	Heinrich 1926	S	15.3	13.5	13.7	15.6	14.6	17.0	—	—
<i>Acleris</i>	Razowski 1966	L	9.4	8.8	—	—	9.7	—	8.8	—
<i>Argyrotaenia</i>	Freeman 1958	S	18.2	17.4	17.5	16.5	—	—	—	—

TABLE 1. Continued.

Genus	Source	Mea- sure	Geographic partition							
			W	E	N	S	NW	SW	NE	SE
Hesperiidae										
<i>Erynnis</i>	Burns 1964	L	17.3	17.6	—	—	—	—	—	—
<i>Hesperia</i>	Lindsey 1942	S	30.5	31.5	30.2	32.0	—	—	—	—
Papilionidae										
<i>Papilio</i>	Tyler 1975	S	76.3	89.2	70.5	79.4	—	73.7	—	86.1
Pyralidae										
<i>Pyrausta</i>	Munroe 1976	L	9.4	7.9	10.4	8.8	—	9.0	—	7.5
<i>Nephoptyx</i>	Heinrich 1956	S	24.7	20.6	—	—	—	—	—	—
Pterophoridae										
<i>Oidaematopho- rus</i>	Barnes & Lindsey 1921	S	24.4	20.1	24.7	24.0	—	—	—	—
Geometridae										
<i>Itame</i>	McGuffin 1972	S	25.2	23.4	—	—	—	—	—	—
<i>Semiothisa</i>	McGuffin 1972	S	24.9	23.2	—	—	—	—	—	—
<i>Anacamptodes</i>	Rindge 1966	L	16.8	14.9	—	—	—	16.5	—	14.8
<i>Nemoria</i>	Ferguson 1969	L	14.0	11.6	—	—	—	13.8	—	11.3
<i>Eupithecia</i>	Bolte 1990	S	20.4	19.0	—	—	—	—	—	—
Noctuidae										
<i>Euxoa</i>	Hardwick 1970	S	35.0	32.7	34.8	36.0	33.8	35.8	—	—
<i>Schinia</i>	Hardwick 1958	S	21.1	17.0	19.7	20.1	—	—	—	—

North-South comparisons, and 6 to 12 comparisons each between Northeast and Northwest, Southeast and Southwest, Northeast and Southeast, and Northwest and Southwest. The surveyed genera are in 18 families and 12 superfamilies. The represented families contain 82 percent of North American Lepidoptera species (Hodges et al. 1983).

Latitudinal Comparisons

Of the 18 genera in North-South comparisons, 10 had means larger in the North, 1 significantly larger; 6 had means larger in the South; and 2 had tied means (Table 1). The frequency distribution of larger means departs little from the equal numbers expected in each main region by chance alone ($P > 0.20$, sign test). This outcome indicates no order-wide directional trend. The lack of trend is repeated in the Northeast-Southeast and Northwest-Southwest comparisons. Of the 12 genera in these subregional comparisons, 6 had means larger in the North, 1 significantly larger; and 6 had means larger in the South (Table 1).

The butterfly genera *Papilio* and *Hesperia* show trends of smaller North body sizes as expected for large-bodied forms, the first one statistically significant (Table 1). The diurnal moth genus *Synanthedon*

shows a null trend (Table 1), an outcome that might be expected for medium sized forms if heat-transfer principles from butterfly investigations apply to other diurnal Lepidoptera. Critical size limits for trend direction in the *Synanthedon* body type are unknown, however.

The two genera with significantly different North and South means, *Elachista* and *Pyrausta*, have the larger mean in the North (Table 1). It is tempting to think that these genera represent northward convergence from small to medium, as expected for small-bodied diurnal forms. Neither genus is diurnal, however. Different and unknown factors probably account for body-size trends among nocturnal genera.

Longitudinal Comparisons

Of the 37 genera in East-West comparisons, 31 had means larger in the West, 15 of them significantly larger; 5 had larger means in the East, 1 of them significantly larger; and 1 had tied means (Table 1). The frequency distribution of larger means in each main region departs sharply from the equal numbers expected by chance ($P < 0.01$, sign test). This outcome suggests an order-wide phenomenon, and matches the published longitudinal trends for species cited in the Introduction. Larger western means are repeated in the Northeast-Northwest and Southeast-Southwest comparisons: of the 20 genera in these subregional comparisons, 16 had means larger in the West, 7 significantly larger; and 4 had indexes larger in the East (Table 1).

If the five surveyed diurnal genera, namely *Synanthedon*, *Carmentis*, *Erynnis*, *Hesperia*, and *Papilio*, are removed from consideration, then an astonishing 30 out of 32 nocturnal genera show larger West means (Table 1). The mean increase in forewing length or span in these genera, computed algebraically, is 16%.

Papilio stands out with its significantly smaller West mean, and *Carmentis*, *Erynnis*, and *Hesperia*—all the remaining diurnal general except *Synanthedon*—show similar but weaker trends (Table 1).

North and South main-regional elevations are subequal at ca. 1000 m; the West regional elevation at ca. 1600 m exceeds the East one by more than 1000 m; and the four subregions follow suit (Table 2). *Papilio* sharply decreases in body size toward the altitudinally higher West (Table 1). Altitudinal decrease also occurs in two strictly western species: *Parnassius phoebus* (Guppy 1986) and *Polites draco* (Brown 1962). Smaller-bodied diurnal genera might remain the same at higher elevations or converge from small to medium. Both trends are evident but weakly expressed among the diurnal genera surveyed. Also, both trends have been previously recorded in individual species: larger body size in *Colias philodice* Godart (Pieridae) (Kingsolver 1983), and no change

TABLE 2. Summary elevations in North America by main regions and subregions. Each value is a mean computed from 50 or more observations chosen systematically with dot-grids from a topographic map.

Main region or subregion	Mean altitude (m)
North	1161
South	939
East	481
West	1619
Northeast	675
Southeast	286
Northwest	1648
Southwest	1591

in *Pontia protodice* (Abbott et al. 1960). Again, critical size limits for trend direction in the body types represented are unknown.

Ultimate reasons for increased body size of nocturnal genera in the West might include one or more of the physical factors varying with altitude, namely atmospheric pressure, evaporation, oxygen pressure, temperature, and solar radiation (Allee & Schmidt 1951). Evaporation also increases with increasing aridity, and there are many desert regions in the West. The influence of physical factors might be direct or indirect. As examples of direct effects, slightly lowered temperature during development sometimes produces larger body size (Miller 1977a, and others), and increased evaporation may select for large body size which favors water retention by decreasing surface/volume ratio (Remmert 1981, and others). Indirect effects might involve food-plant quality, and recent findings make food-plant quality a highly likely explanatory factor. With increasing altitude, plants usually contain more nitrogen per unit of leaf area, sometimes greater concentration of nitrogen, which is associated with greater photosynthetic rate (Körner 1989). Insect body size is known to be directly correlated with amount of dietary nitrogen (Mattson & Scriber 1987). Moreover, body size in a folivorous sawfly has been reported to vary directly with elevation, with nitrogen concentration of the leaves of its food plant varying similarly and simultaneously (Niemelä et al. 1987).

CONCLUSION

Dividing surveyed genera into diurnal and nocturnal helps to order the North American geographic body-size patterns observed. The diurnal genera reveal patterns reasonably consistent with convergence toward medium body size both at higher latitudes and at higher elevations associated with increasing longitudes. The characteristically large-bodied *Papilio* converges toward medium size, perhaps *Hesperia* also, and the medium-bodied genera either do not converge or converge too

little to be detected in this study. No distinctively small-bodied diurnal genera were available in the survey to confirm their convergence toward medium size. Also, the lack of critical size limits for trend direction allows only broad comparisons between actual and expected results.

Among the 32 nocturnal genera surveyed, only *Elachista* and *Pyrausta* show a clear latitudinal body-size trend, both having larger North body sizes. An explanation is doubtless peculiar to these genera. On the other hand, nearly all nocturnal genera increase in body size with increasing longitude, as expected from prior knowledge of Tortricidae increasing in body size with increasing altitude. The regularity of this longitudinal trend suggests a new ecogeographic size rule, but whether it applies beyond moths remains to be investigated.

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